

Relationships between Ecological Pattern and Branching in the Tree Fern *Lophosoria quadripinnata* in Veracruz, Mexico

PAUL ALAN COX

Department of Botany and Range Science, Brigham Young University, Provo, UT 84602

P. B. TOMLINSON

Harvard Forest, Harvard University, Petersham, MA 01366

Pteridophytes often play important roles in determining the nature of plant communities (Watt, 1947). This role is particularly pronounced in tropical cloud forests where the diversity and variety of growth forms in ferns often is very great. In this paper we describe an investigation between the relationship of branching and patterns of shoot distribution in a tree fern.

We chose to study the distribution pattern of shoots of *Lophosoria quadripinnata* (J. Gmelin) C. Chr. (Lophosoriaceae), a small tree fern that occurs throughout the Neotropics (Tryon & Tryon, 1982), and attempted to relate the observed pattern of shoot distribution to the morphology and branching pattern of the species. The shoot morphology of this species has been described superficially by earlier authors. Bower (1926) illustrated a short segment of the axis and showed that the aboveground stems arise from a rhizome. Lucansky (1982) limited his comparison of the anatomy of *Lophosoria* and *Metaxya* to the erect stems. We therefore sought to understand the very prominent role *Lophosoria quadripinnata* plays in cloud forest vegetation by further investigating its morphology and ecology.

METHODS

Previous workers (Tryon et al., 1973) had made extensive maps of pteridophyte vegetation occurring in the cloud forest at Pas de Enriques in the state of Veracruz, Mexico, an area that occurs on the steep slopes of the escarpment of the Sierra Madre Oriental at an elevation of about 1350 meters. The shoot distribution of *Lophosoria quadripinnata* at Pas de Enriques was initially studied by mathematical analysis of these maps; subsequently, field investigations of *Lophosoria quadripinnata* were made and material for morphological analysis was collected.

The original maps compiled by Tryon et al. (1973) were sampled with a paper quadrat scaled so as to yield data comparable with a transect of 32 contiguous meter-square quadrats. In each quadrat, the presence or absence of *Lophosoria quadripinnata* was recorded. Ten transects of this type were analyzed for spatial heterogeneity of shoots using a one-dimensional pattern analysis, a variation of the two-dimensional technique described by Greig-Smith (1957). First, a variance was calculated for the original transect by using the formula

$$\sigma = \frac{\sum_{i=1}^n (x - \bar{x})}{n - 1}$$

where x is the value for *Lophosoria quadripinnata* (1 for present, 0 for absent) in the i th quadrat, \bar{x} is the mean value for all quadrats, and n is the number of quadrats. Since this variance is calculated for samples taken using a meter-square quadrat, the value of the variance is plotted against a 1 meter block size. The 32 quadrat transect is then reanalyzed by considering it to represent 16 contiguous 2 meter by 1 meter quadrats. Presence and absence are then recorded for each of these new rectangular quadrats, and a new variance calculated. The value of this new variance is then plotted on the same graph against a 2 meter block size. The original 32 quadrat transect is then considered to consist of 8 contiguous 4 meter by 1 meter quadrats. Presence and absence are calculated for each of these 4 meter by 1 meter quadrats, and the new variance is then plotted against an 8 meter block size. This procedure is then repeated for a 16 meter block size. The resulting graphs (Fig. 1) yield significant information concerning shoot distribution, for a peak in the graph indicates significant spatial heterogeneity or pattern at that particular block size (Greig-Smith, 1957).

Subsequent to the analysis of the maps, field studies of a population of *Lophosoria quadripinnata* were conducted at Pas de Enriques. Erect shoots were not found to be uniformly distributed in the vegetation, but instead were grouped into distinct clumps or patches, each clump appearing in the vegetation as a dense mass of leaves. The maximum dimensions parallel and perpendicular to the fall line for 10 such patches were recorded. In addition, a large patch was completely excavated and a map of the rhizome system indicating all erect and horizontal shoots was drawn. The unearthed rhizome system then was sectioned, color-coded for reassembly, washed, photographed, preserved in FAA, and analyzed in the laboratory.

Approximately two weeks later the rhizomes were sequentially sectioned and filmed in frame-by-frame analysis. Each sawn surface was photographed by means of a cine camera after it was planed on a radial-arm saw in a modification of the basic cinematographic technique described by Tomlinson (1970) and Zimmermann (1976). The resulting motion picture was analyzed for details of morphology, including branching of axes, and anatomy, including stelar pattern characterizing leaf and branch insertion.

RESULTS

Eight of the ten transects indicated significant ecological pattern as shown in Figure 1 which consists of graphs of transect variances plotted against block sizes. The mean block-size at which significant pattern occurs was found to be 4.25 meters. Of the remaining two transects, one did not exhibit pattern at any block size for *Lophosoria* and the other did not include any *Lophosoria* trunks.

The rhizomatous growth of *Lophosoria* appears to be one of the major factors generating the observed ecological pattern. Although large patches measuring

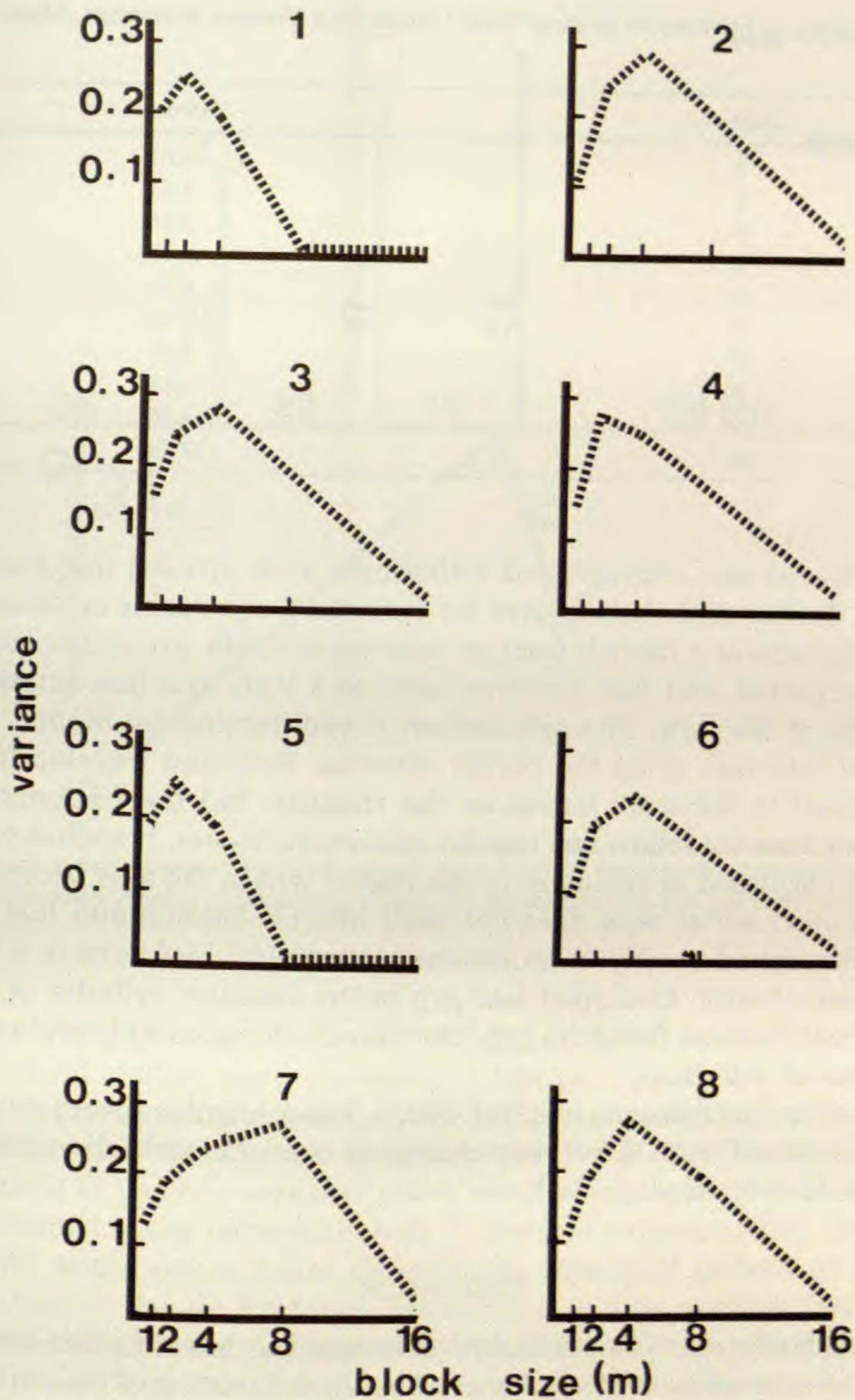


FIG. 1. Analysis of pattern of *Lophosoria quadripinnata* at Pas de Enriquez, Veracruz, Mexico, for eight transects. For each graph block size is plotted along the x axis while variance is plotted against the y axis.

up to 19 meters in diameter and occupying over 280 square meters were recorded, the mean diameter of a *Lophosoria* patch as measured in the field (Table 1) is 5.97 meters, a value that would be detected in the pattern analysis as a peak at a block size of either 4 or 8 meters.

Our morphological analysis confirms that *L. quadripinnata* has a dimorphic shoot system consisting of underground plagiotropic axes (rhizomes) that bear

TABLE 1. Diameters of *Lophosoria quadripinnata* Clones on a Vertical Projection. Mean = 5.97 m; s.d. = 5.18 m.

Clone #	Diameter
1	2.75
2	4.90
3	2.97
4	1.47
5	5.20
6	2.70
7	4.87
8	12.56
9	4.40
10	17.89

only scale leaves and aboveground orthotropic axes (trunks) that bear foliage leaves (Fig. 2). The scale leaves have no indication of a rachis or a blade. Each rhizome originates as a branch from an existing rhizome, grows horizontally for an extended period, and then becomes erect as a leafy axis that emerges as the visible trunk of the fern. The sympodium is proliferated by branch rhizomes that arise at intervals along the parent rhizome. Branches develop from buds located abaxial to the scale leaves on the rhizome, but the frequency of bud development does not follow any regular pattern. However, branches occur most often at the distal end of rhizomes in the region where the axis becomes orthotropic. The erect aerial stem does not itself branch. Branch and leaf insertion can be distinguished readily in transverse section. The leaf trace of a scale leaf makes a characteristic U-shaped leaf gap in the vascular cylinder of the stem, while the branch trace forms no gap, the branch being completely solenostelic from its level of initiation.

Phyllotaxis in the rhizome is spiral with a mean angular divergence of 135.4 degrees ($n = 69$, s.d. = 28.5) but may change in axes that exhibit transition from plagiotropic to orthotropic growth.

DISCUSSION

The analysis of pattern is a valuable technique for detecting non-randomness in the spatial arrangement of vegetation. The determination of the scale or block size at which significant pattern occurs allows hypotheses to be made concerning factors that control that pattern. In our study of *Lophosoria quadripinnata*, we found significant pattern to exist at a mean block size of 4.25 meters. Since no features of the terrain or soils of the site were known to exhibit a pattern at that level and since none of the other pteridophyte species recorded by Tryon et al. (1973) showed pattern at that level, we hypothesized that exogenous factors were not responsible for the pattern detected in *L. quadripinnata*. Our hypothesis instead was that an endogenous factor, specifically a rhizomatous growth habit, was responsible for the detected pattern. However recent workers (Lucansky, 1974, 1982; Lucansky & White, 1974) had not studied decumbent axes in *L. quad-*

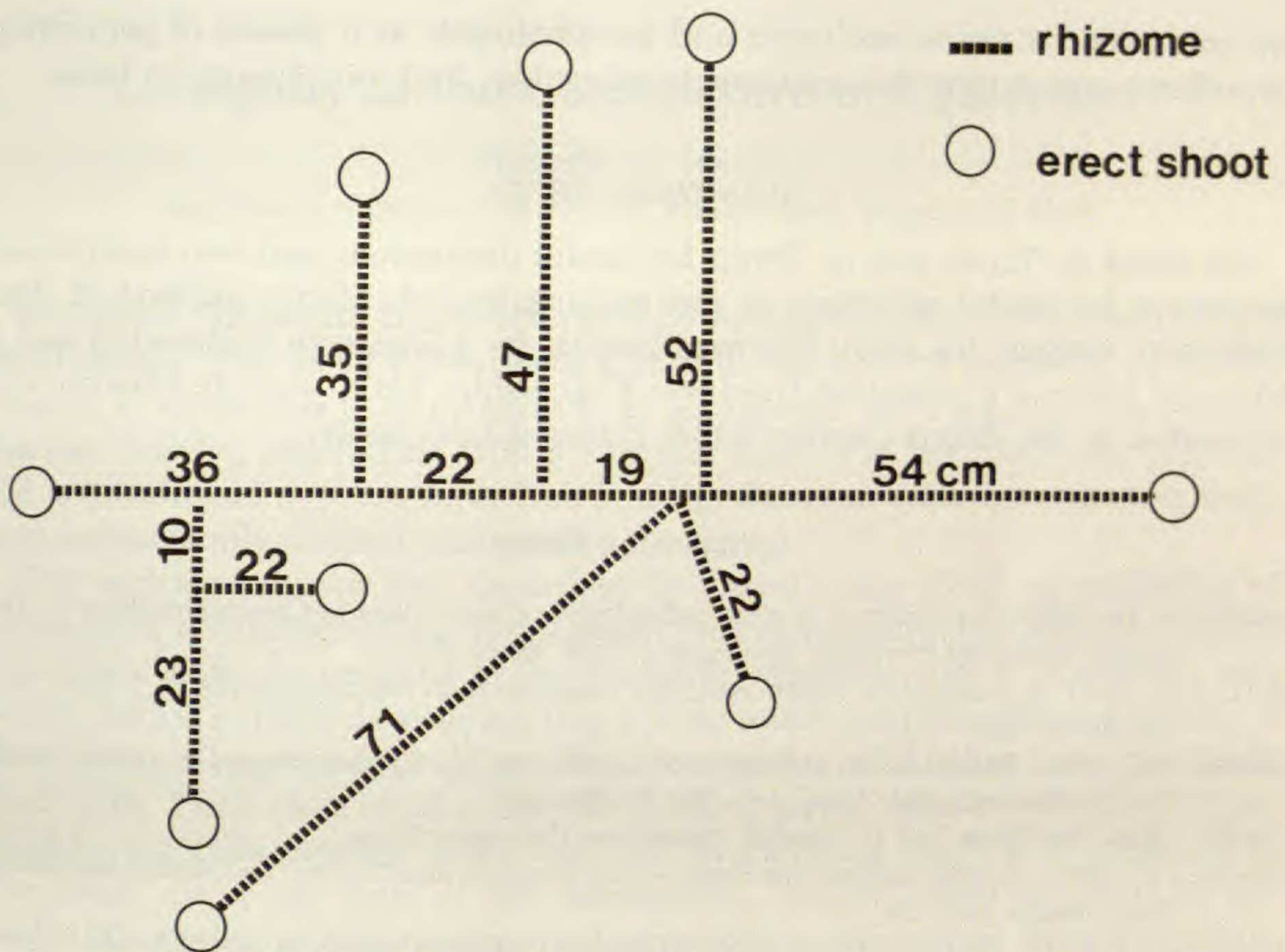


FIG. 2. Diagrammatic map of rhizome system excavated of *Lophosoria quadripinnata*. Distances given in centimeters. Angles of branching shown are stylized and do not represent actual divergence of branches.

ripinnata although Bower (1926, p. 286; 1912, p. 293) was aware of their existence. Therefore field studies were necessary to test our hypothesis that rhizomatous growth is a prominent feature of *L. quadripinnata* growth. Our studies confirmed the existence of a rhizomatous growth pattern in *L. quadripinnata* while the measurement of patches revealed patch size to be consistent with the scale of pattern detected in our pattern analysis. It therefore appears likely that rhizomatous growth is the major factor determining ecological pattern of *Lophosoria quadripinnata* at Pas de Enriques. However it is also possible that patch size and pattern reflect some unknown feature of sexual reproduction (Conant & Cooper-Driver, 1980); this alternative cannot be tested with our data.

Rhizomes are known from other tree fern genera such as *Cyathea sternbergii* Pohl (Brade, 1971) and *Alsophila marriana* (Hook.) Tryon (Hallé, 1966) while *Cyathea parvula* (Jenm.) Dunim produces negatively geotropic branches that root when they reach the soil (Tryon & Tryon, 1982). It is not known how these features affect their ecological pattern.

Pattern analysis has not been used previously in ecological studies of pteridophytes with the exception of Anderson's (1961) work on *Pteridium aquilinum* in North Wales. That study is notable in that it examines the overall pattern of clonal development of fern rhizomes (cf., Bell & Tomlinson, 1980). Certainly pattern analysis has proven useful in our study of *Lophosoria quadripinnata* and

we commend its use to ecologists and morphologists as a means of generating hypotheses concerning the relationship of ecology and morphology in ferns.

ACKNOWLEDGMENTS

We thank R. Tryon and A. Tryon for useful discussions and two anonymous reviewers for useful criticisms of our manuscript. M. Moore assisted in data collection. During this study Cox was funded by a Danforth Fellowship and a National Science Foundation Graduate Fellowship. Field work in Mexico was supported by the Atkins Garden Fund, Harvard University.

LITERATURE CITED

- ANDERSON, D. 1961. The structure of some upland plant communities in Caernarvonshire. I—The pattern shown by *Pteridium aquilinum*. *J. Ecol.* 49:369-377.
- BELL, A. D. and P. B. TOMLINSON. 1980. Adaptive architecture in rhizomatous plants. *J. Linn. Soc., Bot.* 80:125-160.
- BOWER, F. O. 1912. Studies in the phylogeny of the Filicales. IV. *Lophosoria* and its relation to the Cyatheoidea and other ferns. *Ann. Bot.* 26:269-324.
- . 1926. *The ferns*. Vol. II. London: Cambridge University Press.
- BRADÉ, A. C. 1971. *Cyathea sampaioana* Bradé et Ras. Somente uma "forma" de *Cyathea sternbergii* Pohl. *Bradea* 10:73-76.
- CONANT, D. S. and G. COOPER-DRIVER. 1980. Autogamous allohomoploidy in *Alsophila* and *Nephrolepis* (Cyatheaceae): a new hypothesis for speciation in homoploid homosporous ferns. *Amer. J. Bot.* 67:1269-1288.
- GREIG-SMITH, P. 1957. *Quantitative plant ecology*. London: Butterworth.
- HALLÉ, F. 1966. Étude de la ramification du tronc chez quelques fougères arborescentes. *Adansonia* 6:405-424.
- LUCANSKY, T. W. 1974. Comparative studies of the nodal and vascular anatomy in the neotropical Cyatheaceae. I. *Metaxya* and *Lophosoria*. *Amer. J. Bot.* 61:472-480.
- . 1982. Anatomical studies on the neotropical Cyatheaceae. II. *Metaxya* and *Lophosoria*. *Amer. Fern J.* 72:19-29.
- and R. A. WHITE. 1974. Comparative studies of the nodal and vascular anatomy in the neotropical Cyatheaceae. III. Nodal and petiole patterns: summary and conclusions. *Amer. J. Bot.* 61:818-828.
- TOMLINSON, P. B. 1970. Monocotyledons: towards an understanding of their morphology and anatomy. Pp. 207-292 in *Advances in botanical research*, Vol. 3, ed. R. D. Preston. London: Academic Press.
- TRYON, R., B. VOELLER, A. TRYON, and R. RIBA. 1973. Fern biology in Mexico. *BioScience* 23:28-32.
- and A. TRYON. 1982. *Ferns and allied plants, with special reference to tropical America*. New York: Springer-Verlag.
- WATT, A. 1947. Contributions to the ecology of bracken. IV. The structure of the community. *New Phytol.* 46:97-121.
- ZIMMERMANN, M. H. 1976. The study of vascular patterns in higher plants. Pp. 221-235 in *Transport and transfer processes in plants*, eds. I. E. Wardlaw and J. B. Passioura. New York: Academic Press.